

# MORPHOLOGICAL VARIATION AND SYNOPSIS OF THE *MUHLENBERGIA REPENS* COMPLEX (POACEAE)

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## ABSTRACT

The *Muhlenbergia repens* complex consists of rhizomatous perennial species with short contracted inflorescences and awnless spikelets. A study was undertaken to determine the amount of morphological variation that is present within and among the species. Examination of morphological variation has shown that *M. plumbea* does not have a close affinity with other species of the complex. *Muhlenbergia richardsonis* and *M. squarrosa* were not found to be morphologically distinct and are considered a single highly variable species most closely related to *M. repens* and *M. utilis*. Morphological variation between *M. villiflora* and *M. villosa* intergrades to a large extent, although they remain distinct throughout most of their distribution, and they are thus recognized as a single species with two varieties, var. *villiflora* and var. *villosa*. A key to the six species and two varieties is provided.

## RESUMEN

El complejo *Muhlenbergia repens* está formado por especies rizomatosas perennes con inflorescencias cortas contraídas y espiguillas místicas. Se realizó un estudio para establecer la variación morfológica intraespecífica e interespecífica. El examen de la variación morfológica ha mostrado que *M. plumbea* no tiene afinidades grandes con las otras especies del complejo. Se encontró que *Muhlenbergia richardsonis* y *M. squarrosa* no son distintas morfológicamente y son consideradas como una sola especie de variabilidad alta, más afín a *M. repens* y *M. utilis*. La variación morfológica entre *M. villiflora* y *M. villosa* se intergrada en una gran extensión aunque permanecen diferentes en la mayor parte de su distribución, y por ello se reconocen como una única especie con dos variedades, var. *villiflora* y var. *villosa*. Se ofrece una clave de las seis especies y las dos variedades.



## INTRODUCTION

The genus *Muhlenbergia* Schreb., with about 160 species, has a center of distribution in the southwestern United States and northern Mexico. In general, these species are found in hot, arid habitats although some species occur in diverse situations such as moist shaded woodlands (*M. schreberi* Gmel. and its allies) and alpine meadows [*M. richardsonis* (Trin.) Rydb. and *M. filiformis* (Thurb.) Rydb.]. Members of the *Muhlenbergia repens* complex (Morden & Hatch 1987) are distributed throughout North America (excluding the southeastern United States) and in the Andean Highlands of South America. This complex is characterized by a rhizomatous perennial habit, short culms seldom exceeding 40 cm, short involute leaf blades, and a short contracted inflorescence with awnless or mucronate spikelets. As presently understood, this complex consists of eight species which may be placed into two groups based on floret vestiture. Six species are typically considered to have glabrous spikelets, several of which are minutely pubescent or scabrous on the lemma when observed closely (above 20× magnification). These include *M. repens* (Presl) Hitchc., *M. utilis* (Torr.) Hitchc., *M. richardsonis* (Trin.) Rydb., *M. squarrosa* (Trin.) Rydb., *M. fastigiata* (Presl) Henrard, and *M. plumbea* (Trin.) Hitchc. Two species, *M. villiflora* Hitchc. and *M. villosa* Swallen, have florets that are densely villous on both the lemma and palea. *Muhlenbergia plumbea*, which typically grows larger than is usual for this complex and often has an open inflorescence, is included in this complex upon the suggestion of Charlotte Reeder (pers. comm.). Most of the species occur in the southwestern United States or adjacent Mexico.

The species of the *M. repens* complex have been traditionally separated into two groups on the basis of glabrous or villous florets (Hitchcock 1950; Gould 1975). Analysis of these species using scanning electron microscopy (SEM) found that only three of the species (*M. fastigiata*, *M. plumbea*, and *M. utilis*) are completely devoid of vestiture on the floret, whereas all others have macrohairs present on the lemma and/or palea (Morden 1985). Both *M. villiflora* and *M. villosa* have copious macrohairs evident without the aid of magnification. However, *M. repens*, *M. richardsonis*, and *M. squarrosa* all have macrohairs, albeit smaller and in much lower frequency than *M. villiflora* and *M. villosa*, distributed on the lemma and palea in a pattern similar to that of the densely villous species (near the base of the lemma and between the two nerves of the palea). Of these three species, macrohairs of *M. repens* are typically longer and more densely distributed over the callus of the floret and the lemma and palea. In some populations the hairs are visible at 20× magnification with a dissecting microscope. Macrohairs of *M. richardsonis* and *M. squarrosa* are shorter and less frequent, and were seen only with SEM.



Little is known of the variation among the taxa of this complex. Morden and Hatch (1987) studied the variation present within leaf anatomical traits and found that all species of this complex were discernible with the exception of *M. richardsonis* and *M. squarrosa*. There is an apparent overlap in morphological characters and sympatry in distribution (occasionally growing side by side). In one instance, three different species of this complex were found growing within a five square meter area. Morphological characters which have often been used to separate species within this complex often show considerable variation. For example, of the species with glabrous florets, only *M. richardsonis* and *M. squarrosa* were reported to have nodulose roughening on the culms. However, upon close inspection this is found to a limited degree in all species of the complex. Further, it is not uncommon within some populations for the lower branches of the inflorescence to become relaxed, and in some cases reflexed, similar to what is found in *M. plumbea*, although most taxa typically have contracted panicles.

There are two problematic species groups within this complex. In one, *M. richardsonis* and *M. squarrosa* have been found throughout North America north of Mexico (including Alaska and the provinces of Canada) except in the southeastern United States. They have previously been reported as separate species based on culm morphology or as a single species (under *M. richardsonis*; Cronquist et al. 1977); *M. squarrosa* has stout, decumbent, and spreading culms and occupies drier sites with little competition from other species, whereas *M. richardsonis* has more slender, erect culms and is usually growing in moister soils in a meadow-like association. The South American species, *M. fastigiata*, appears similar to *M. squarrosa* and *M. richardsonis* in all characters except that the vegetative morphology is depauperate. This species occurs in the Andean Highlands of Argentina, Bolivia, and Peru, and is not found below 3000 meters elevation. Given the broad distribution of *M. richardsonis* and *M. squarrosa*, and that it often occurs at high elevations in the Rocky Mountains, one previously unexplored possibility is that *M. fastigiata* is a smaller South American form of this species. Although *M. richardsonis* and *M. squarrosa* are apparently morphologically distinct from others of the complex, they are most similar to and apparently intergrading in some regions of their range with *M. repens* (in the southwestern United States) and *M. utilis* (in Texas and California). As a result of the similar morphology herbarium specimens are frequently misidentified.

The second problematic species group includes *M. villiflora* and *M. villosa*. *Muhlenbergia villiflora* forms extensive stands across gypsiferous soils in northern Mexico and is a dominant component of that ecosystem. In contrast, *M. villosa* is found in very localized populations on alkaline and calcareous soils of western Texas and adjacent New Mexico. The nature of the rela-



tionship between these two species has not been previously explored, and the paucity of populations of *M. villosa* available for comparison (four prior to this study) has made population studies difficult.

A morphological analysis of the *M. repens* complex was undertaken to elucidate biological relationships among the species. A key and descriptions to the taxa are presented based upon population studies and results of analysis of anatomical variation (Morden & Hatch 1987).

#### MATERIALS AND METHODS

Field collections were made during the flowering periods of the species (August through October) in the northern states of Mexico, the southwestern United States, and the Sierra Nevada and Rocky Mountains. To insure isolation between populations, a minimum distance of 10 miles was traveled between successive collection sites. In most cases, ten independent specimens from each site were semi-randomly collected and pressed; selection was biased in favor of mature plants that did not show any signs of damage from insects, herbivores, trampling, etc. As always with rhizomatous species, the possibility exists that a population is made up of a single clone with specimens displaying mosaic or somatic variation rather than individual genetic variation. Therefore, specimens were collected far enough apart (e.g. 2 meters) within any single population to avoid this possibility. In addition, herbarium specimens on deposit in several herbaria were used to represent species we were not able to collect. In some cases, sufficient material of a single collection was available to serve as a "real" population; in other cases, "artificial" populations were made by selecting specimens from the same geographic region and grouping them together. A total of 117 populations (real and artificial) were available for analysis. Vouchers for the population study are deposited at the S.M. Tracy Herbarium (TAES).

Table 1 lists the 34 characters identified that show variation among the populations analyzed. Several characters show variations unique to this complex and warrant further description. Plants in this complex are often decumbent at the base, and as such culm height will represent culm length. Culm nodules were counted within a 5 mm distance in one surface view of the culm, generally below the inflorescence. Leaf blade curvature was recorded as a two state character and observed as straight or arcuate; degree of leaf longitudinal posture was recorded as a multistate character and recorded as flat, involute, or folded. Spikelet length was measured from the base of the spikelet to the apex of the lemma (or the glume if they exceeded the lemma) excluding the lemma awn. Occasionally, a second floret was associated with the floret, and was measured but excluded from the analysis. Vestiture of the lemma and palea was recorded as a four state character:



TABLE 1. Thirty-four characters used to assess morphological variation in the *M. repens* complex. All characters were measured for continuous variation except those labeled as binary state (BS) or multistate (MS).

<b>Vegetative:</b> rhizome diameter, rhizome scale length, culm height, culm diameter, culm internode length, culm nodules (MS), leaf sheath length, culm/sheath ratio, ligule length, leaf blade length, leaf blade width, leaf blade curvature (BS), degree of leaf longitudinal posture (MS).
<b>Inflorescence:</b> inflorescence length, inflorescence width, nodes per inflorescence (MS), branches per node (MS), inflorescence branch length, inflorescence branch angle (MS), spikelets per inflorescence branch (MS), pedicel length.
<b>Spikelet:</b> spikelet length, first glume length, first glume nerves (MS), second glume length, second glume nerves (MS), lemma length, lemma awn length, lemma vestiture (MS), palea length, palea vestiture (MS), anther length, caryopsis length, caryopsis width.

glabrous, scabrous or minutely pubescent, with distinct trichomes (although short and/or sparse), and densely villous.

Univariate statistics (mean, standard deviation and range) were performed using SAS computer packages (Goodnight 1979). A nested analysis of variance (ANOVA) was done to compare intrapopulation, interpopulation, and interspecies variation. Multivariate statistics of principal components analysis (PCA) and cluster analysis were performed using the NT-SYS package of Rohlf et al. (1980). Principal components were derived using the correlation matrices; cluster analysis used the unweighted pair group method using arithmetic averages (UPGMA) on both correlation and distance matrices. To assess the degree of divergence among populations, the multivariate analysis of variance (MANOVA) and canonical analysis programs in SAS were used.

RESULTS AND DISCUSSION

Initially, all populations were analyzed with PCA and MANOVA to determine various groupings within the complex. Results from PCA indicated that all populations, except the nine populations of *M. plumbea*, cluster together. By analysis of eigenvector coefficients, the characters identified as contributing to the separation of these two groups were culm nodules (absent in *M. plumbea*, but present in all other species of the complex at least to a limited degree), leaf blade longitudinal posture (always folded in *M. plumbea* and flat or involute in other species), and inflorescence width. Two additional groupings were evident when all populations, excluding those of *M. plumbea*, were analyzed using PCA: populations with prominently villous florets in the spikelet were clearly separated from those with glabrous or scabrous florets. Results of an analysis of all populations using MANOVA in which the three groups just described are presented in



Figure 1. Because *M. plumbea* is so clearly distinguishable from the other species of the complex it was not considered in further population analyses. Soderstrom (1967) suggested the leaf anatomy of *M. plumbea* might be more closely related to *M. uniflora* or *M. arizonica*, a placement in which we are in agreement. Based on the results found here for all species of the complex, the remaining species will be discussed in their traditional groupings of "glabrous" taxa (macrohairs on the floret absent or not readily evident without magnification) and "villous" taxa (copious macrohairs evident without magnification).

*Glabrous taxa.*—Five taxa with "glabrous" florets (*M. fastigiata*, *M. repens*, *M. richardsonis*, *M. squarrosa*, and *M. utilis*), were identified in the initial analysis. An ANOVA and PCA were used to determine which characters accounted for most of the variation in distinguishing among populations. The characters identified were ligule length, spikelet length, first and second glume length, lemma length, lemma vestiture, palea length and caryopsis length. Populations of *M. richardsonis* and *M. squarrosa* are not consistently distinguishable from one another (Fig. 2) on the basis of morphological characters analyzed. This was also corroborated using cluster analysis and MANOVA (Morden 1985) and henceforth will be referred to as a single species, *M. richardsonis*. Populations of *M. utilis* and *M. repens* appear to be clearly distinguishable from those of *M. fastigiata* and *M. richardsonis* whereas populations of *M. fastigiata* and *M. richardsonis* appear to intergrade in morphological form.

To investigate this last point in more detail, analyses were performed on populations of *M. fastigiata* and *M. richardsonis* to determine the extent to which these species are similar. The results of PCA (Fig. 3) and cluster analysis (Morden 1985) clearly show these populations to be distinct. Characters which consistently distinguish these populations are plant size (culm height, internode length, and inflorescence length) and floret vestiture (*M. fastigiata* being completely glabrous whereas *M. richardsonis* is usually scabrous or minutely pubescent). Inflorescence length and floret vestiture are of particular importance because they may be indicative of a more conservative distinction between the two species, whereas differences based only on plant size may be environmentally induced.

A cluster analysis using UPGMA was performed on all four of these taxa. Characters which did not account for variation among the taxa as determined from analysis of variance and PCA were eliminated from the analysis. These results indicate that the "glabrous" taxa are represented by four distinct groups, each of which is separated from the others based on morphological characters (Fig. 4). The cluster analysis also depicts *M. richardsonis* being more closely aligned with *M. repens* rather than *M. fastigiata* as was previously hypothesized. The alignment of *M. fastigiata* and *M.*



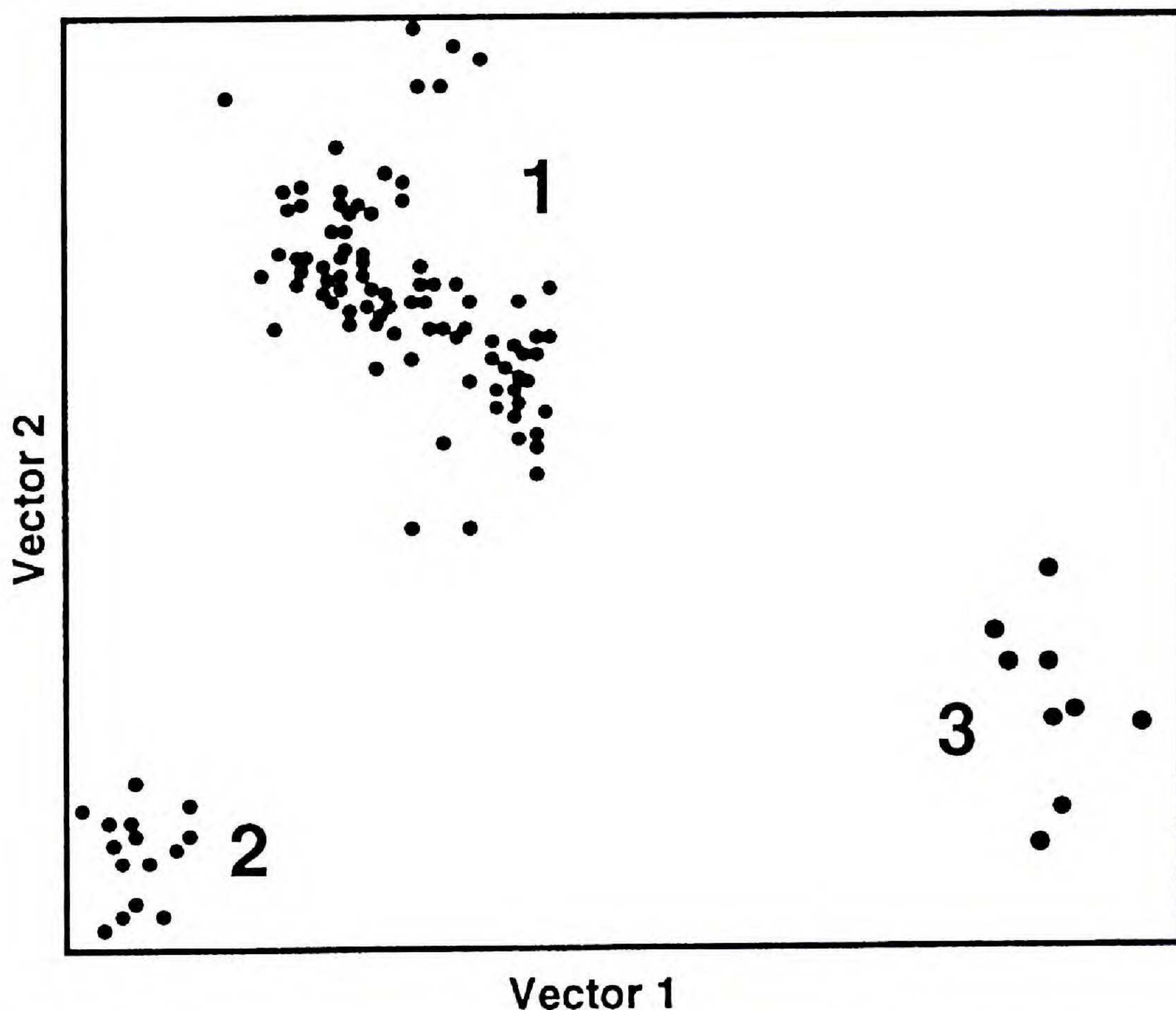


FIG. 1. Two dimensional representation of all populations of the *M. repens* complex analyzed with MANOVA. Clusters 1, 2, and 3 represent glabrous taxa, villous taxa, and *M. plumbea*, respectively.

*utilis* here may not be entirely unexpected; both species have completely glabrous florets and similar spikelet size, although vegetatively they are very distinct.

*Villous taxa.*—An ANOVA and PCA of the 15 population samples of species with distinctly villous florets, *M. villiflora* and *M. villosa*, identified ten characters for which there is relatively high level of variation at the species level. These characters were ligule length, leaf blade length, inflorescence branch length and spikelets per inflorescence branch, spikelet length, first and second glume length, lemma and palea length, and caryopsis length. The first two components in the PCA (Fig. 5) accounted for 63.4% of the variation present.

Most of the populations segregated by species classification within the plot. However, three populations of special interest include *Morden 514* ("a"; Fig. 5) *Valdes s.n.* ("b"), and *Spellenberg 4565* ("c"). Samples of *Morden 514* and *Valdes s.n.*, were collected at the same locality (Rancho Experimental "Los Angeles") in southern Coahuila during different seasons. Analysis of the specimens in *Morden 514* showed that these plants were very



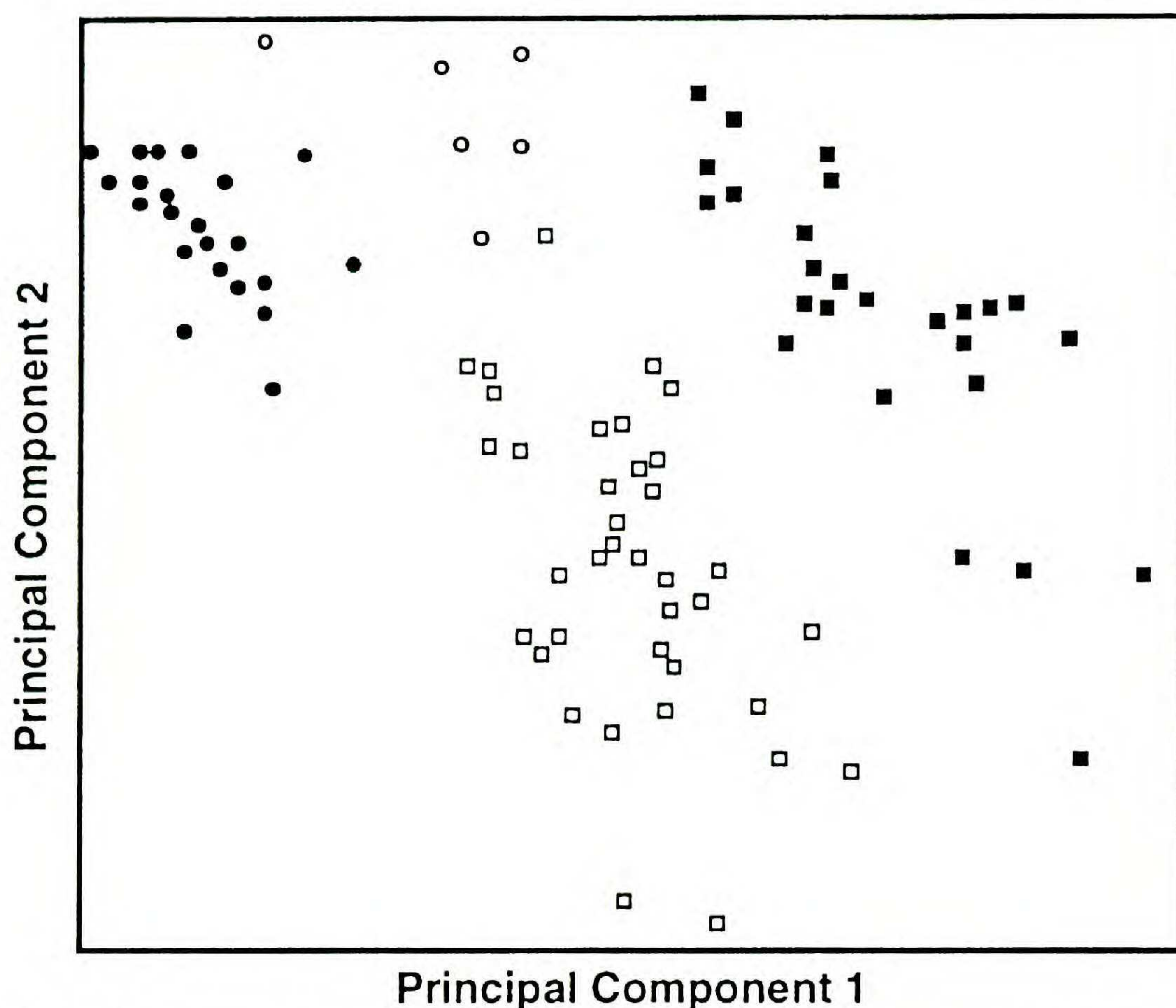


FIG. 2. Principal components analysis of populations of the "glabrous" taxa using all characters measured. The symbols present represent the species *M. repens* (■), *M. utilis* (●), *M. richardsonis* (○), and *M. fastigiata* (□). The first and second axes accounted for 53.2% of the variation.

typical of *M. villiflora* whereas those of population *Valdes s.n.* were more similar to those of *M. villosa* and clustered with them in the analysis. The distinguishing characteristic between these two species has been plant size; *M. villosa* is larger than *M. villiflora* in most morphological characters. It is evident that there exists enough plasticity in these populations that under different growing conditions the plants can exhibit the characters of the other group.

The *Spellenberg 4565* collection segregated from the rest of *M. villosa* in a way that indicated it was very distinct from other populations of this species. In analyzing individual specimens of this population, it was apparent that they represent a larger form with longer leaf blades and sheaths, longer internodes, and more nodes in the inflorescence than is typical of the species. Results of cluster analysis (Morden 1985) also show this population as segregating distinctly from the remainder of the populations.

These results support the conclusion that *M. villiflora* and *M. villosa* can not be consistently separated on the basis of morphological characters and



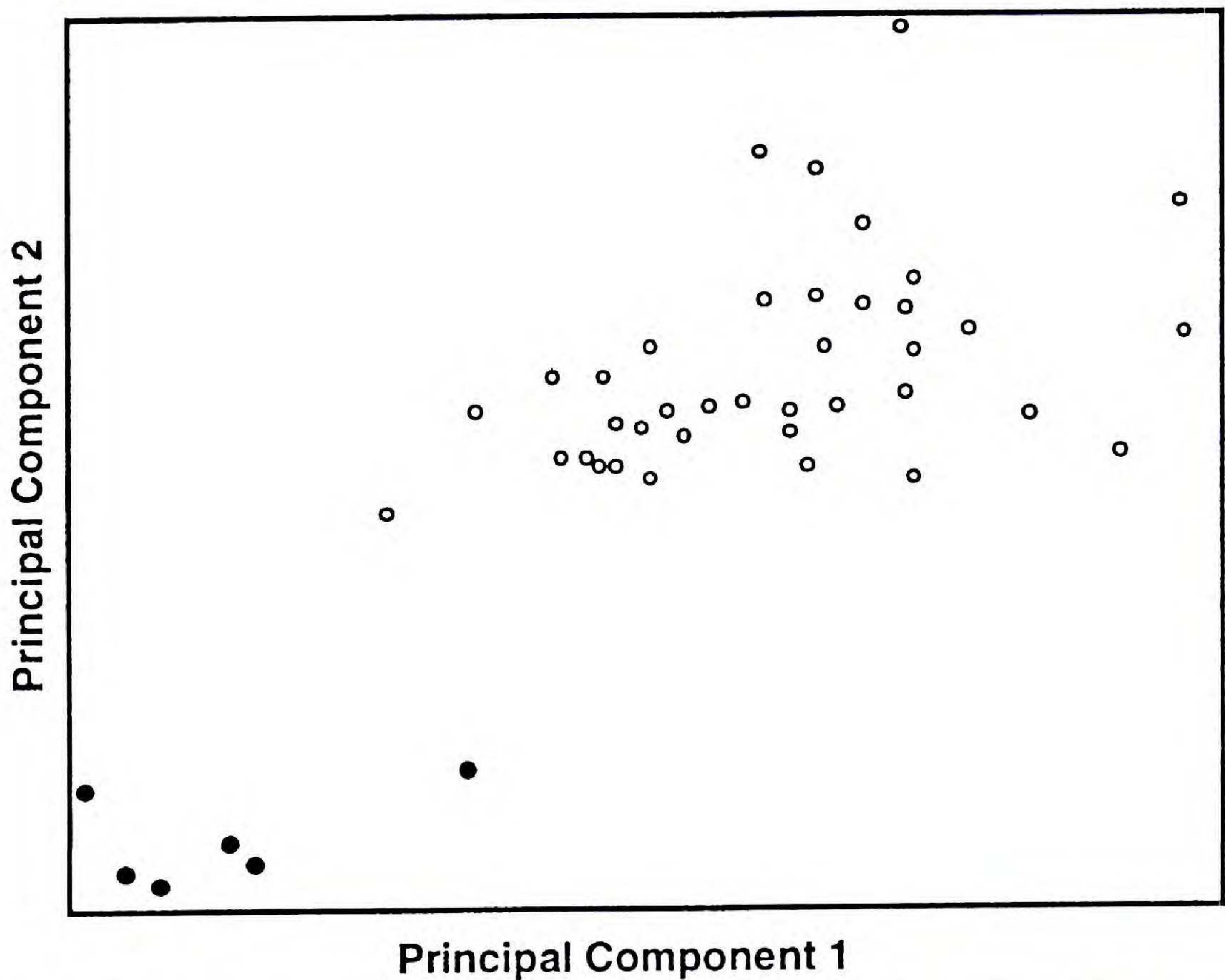


FIG. 3. Principal components analysis of populations of *M. richardsonis* (○) and *M. fastigiata* (●). The first and second axes accounted for 54.1 % of the variation.

as such should be regarded as a single species. In general, *M. villosa* tends to be larger than *M. villiflora* and occupies a different habitat (alkaline and calcareous versus gypsiferous soils, respectively). As such, they have been treated as distinct varieties under *M. villiflora* (Morden 1996). However, these differences may be a result of phenotypic variability induced by the different habitats. *Spellenberg 4565* may also represent a distinct variety that is geographically isolated from other populations. However, we refrain from taxonomic recognition of this form until more information about the population is obtained. Subsequent trips to the collection region by the first author, R. Spellenberg (New Mexico State Univ., pers. comm.), and others have failed to rediscover it, thus its true status may never be revealed.

KEY TO THE SPECIES

- 1. Inflorescence open, lower panicle branches usually greater than 5.5 cm long; leaf blades folded or flat, prominent midvein present. .... 2. *M. plumbea*
- 1. Inflorescence contracted, lower panicle branches usually less than 5 cm long, rarely open or reflexed; leaf blades flat or involute, a prominent midvein absent.
- 2. Lemma and palea densely villous.



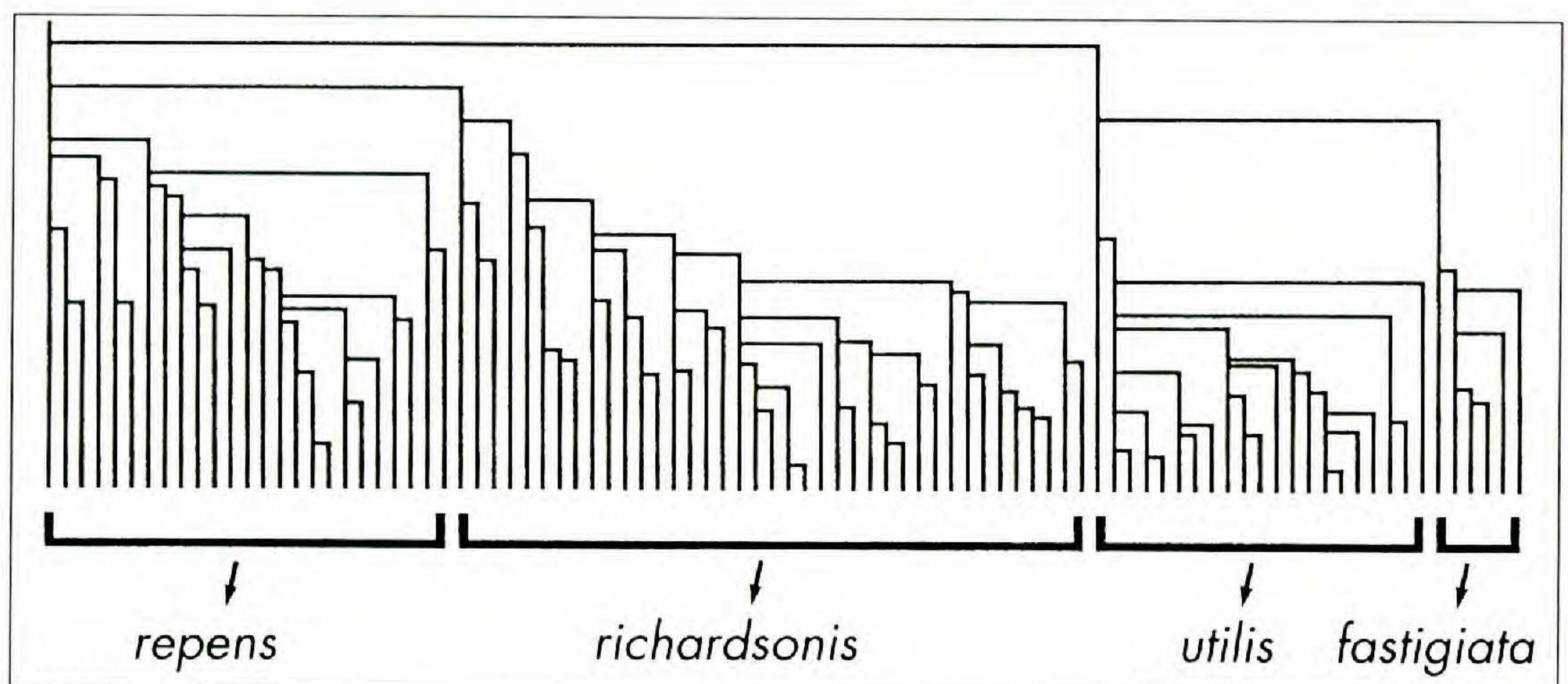


FIG. 4. Cluster analysis of the "glabrous" taxa from the distance matrix with all extraneous characters removed from the analysis.

3. Spikelets usually less than 2.0 mm long; plants of gypsiferous soils of northern Mexico ..... 6a. *M. villiflora* var. *villiflora*
  3. Spikelets usually greater than 2.0 mm long; plants of alkaline or calcareous soils, west Texas and New Mexico ..... 6b. *M. villiflora* var. *villosa*
  2. Lemma and palea glabrous or scabrous, not densely villous.
  4. Mature spikelets 2.7 mm long or greater; glumes greater than 1/2 the length of floret; lemma tapering to a mucro or short awn ..... 3. *M. repens*
  4. Mature spikelets less than 2.7 mm long, seldom greater; glumes 1/2 or less than length of floret; lemma awnless or mucronate, not tapering.
  5. Ligule less than 0.6 mm long, seldom to 0.8 mm; inflorescence, at least basally, usually included in uppermost culm sheaths ..... 5. *M. utilis*
  5. Ligule greater than 0.7 mm long, seldom less; inflorescence usually on an exserted peduncle.
  6. Plants usually less than 10 cm tall; leaves less than 9 mm long; lemma completely glabrous: Andean highlands ..... 1. *M. fastigiata*
  6. Plants seldom less than 15 cm tall. leaves greater than 10 mm long; lemma scabrous or minutely pubescent, at least apically; North America ..... 4. *M. richardsonis*
1. ***Muhlenbergia fastigiata* (J. Presl) Henrard, Meded. Rijks-Herb. 40:59. 1921. BASIONYM: *Sporobolus fastigiatus* J. Presl, Rel. Haenk. 1:241. 1830. *Vilfa fastigiatus* Meyen, Reis. Erd. 1:484. 1834 (nom. nud.). TYPE: Peruviana? *Haenke s.n.* (HOLOTYPE: PR!; Type fragment: US!).**

Perennial with scaly rhizomes; rhizome scales (4.5–)5.5–8.1(–10) mm long, acute, often deteriorating with age. Culms 2–8(–11) cm tall, 2–3(–5) mm diam., mostly erect, branching, glabrous; internodes 1–3(–5) mm long, compressed, nodulose-roughened slightly below inflorescence. Leaves distichous; sheaths 3–6(–8) mm long, overlapping, margins hyaline. Ligules (0.6–)0.7–1.1(–1.4) mm long, membranous, acute or slightly rounded, decurrent. Blades (2–)4–8(–9) mm long, 0.6–1.1 mm wide, involute, arcuate, glabrous, margins scabrous. Inflorescence a panicle, 1–2 cm long, 1–



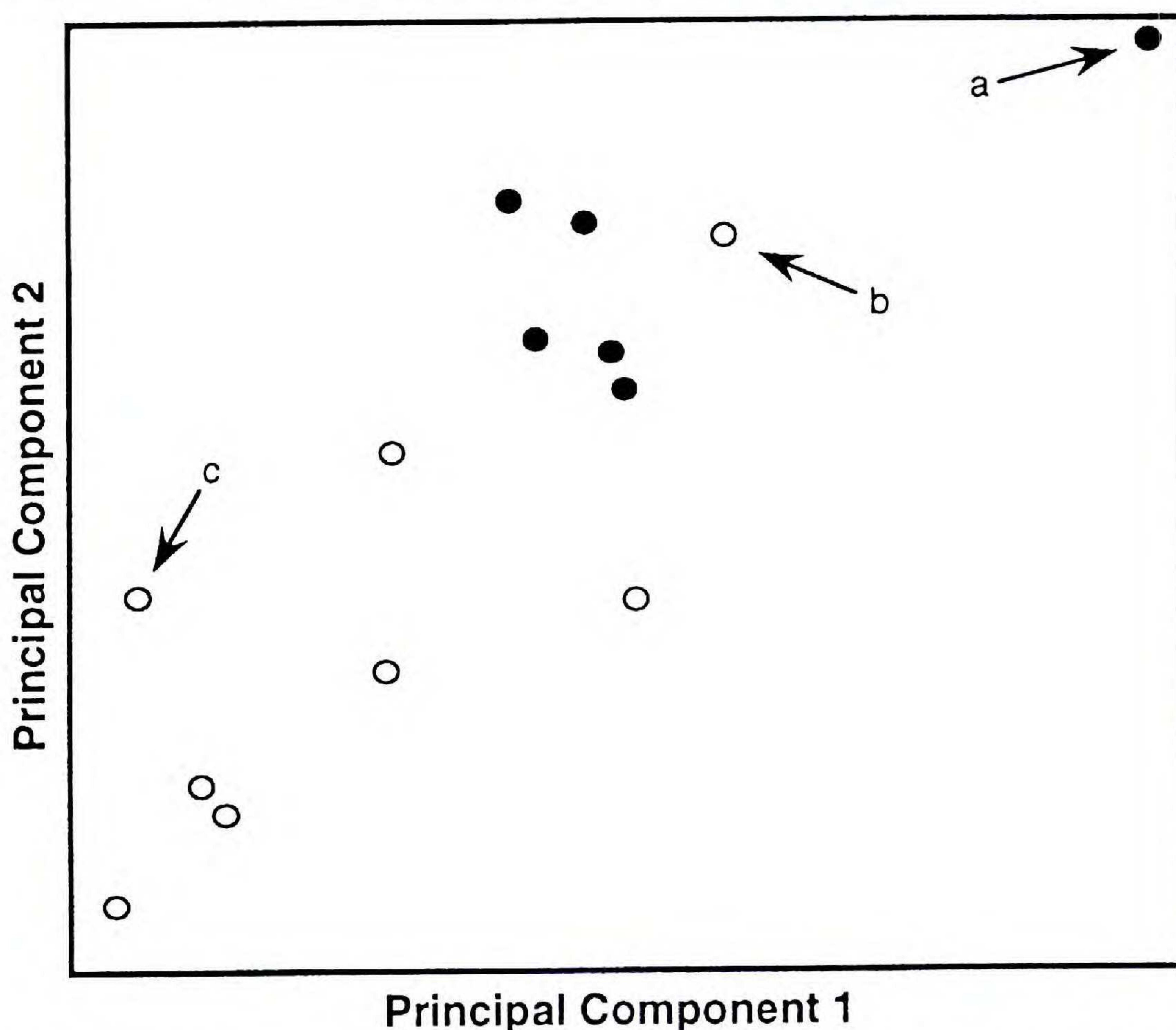


FIG. 5. Principal components analysis of the "villous" taxa, *M. villiflora* (○) and *M. villosa* (●). Populations "a" (Morden 514) and "b" (Valdes y Vasquez s.n.) were collected at the same locality (Rancho Experimental "Los Angeles", Coahuila, Mexico) in different years and growing seasons. Population "c" (Spellenberg 4565) was collected in Otero Co., New Mexico.

3(–4) mm wide, narrow, contracted usually exserted above foliage; inflorescence branches solitary at each node, with 3–7 nodes per inflorescence; branches ascending. Pedicels 0.3–0.8(–1.3) mm long, minutely setose. Spikelets (1.8–)2.0–2.4(–2.5) mm long, usually crowded on branches, 1–5(–8) spikelets on lowermost branches. Glumes (0.8–)1.0–1.4(–1.6) mm long, equal, about one-half the length of spikelet, acute, straw colored to dark green, one-nerved. Lemmas (1.7–)1.9–2.3(–2.4) mm long, 3-nerved, glabrous, narrowing to a mucronate apex, usually dark green. Paleas (1.6) 1.8–2.2(–2.4) mm long, glabrous, dark green. Anthers 0.9–1.6 mm long, yellow. Caryopses ca 1.2 mm long, 0.4 mm wide, narrowly elliptic, dark brown. Chromosome number not reported.

*Distribution*.—Andean highlands of Argentina, Bolivia, and Peru, usually above 3000 m elevation.

*Muhlenbergia fastigiata* resembles *M. richardsonis* in many of its vegetative and reproductive characteristics. However, this species differs from *M.*



*richardsonis* by its short stature, overlapping and distichous leaves, and florets lacking any vestiture.

2. **Muhlenbergia plumbea** (Trin.) Hitchc., Contr. U.S. Natl. Herb. 17:296. 1913. BASIONYM: *Vilfa plumbea* Trin., Mem. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 4(1):98. 1840. *Sporobolus plumbeus* (Trin.) Hemsl., Biol. Centr. Amer. Bot. 3:546. 1885. TYPE: "Mineral del Monte, Schlechtendal" *Schiede s.n.* (HOLOTYPE: LE!; Type fragment: US!). Herbarium labels on the type and fragment bear Schlechtendal's name, however it was probably collected by Schiede and sent to Schlechtendal, and later to Trinius.

Perennial with scaly rhizomes; rhizome scales (7.5–)8.5–13(–16) mm long, acute, often deteriorating with age. Culms 13–34(–51) cm tall, (0.4–)0.8–1.2(–1.4) mm diam., glabrous, freely branching at lower culm nodes; internodes 4–40(–60) mm long, variable, smooth, not nodulose-roughened, nodes green or purple, constricted. Sheaths (10–)15–32(–51) mm long, shorter or longer than internode, margins hyaline. Ligules 0.3–0.5(–0.7) mm long, membranous, truncate, decurrent. Blades (1.7–)3–7(–10) cm long, (1.1–)1.6–2.4(–3.0) mm wide, glabrous, flat or folded along a prominent midvein. Inflorescence a panicle, (4–)5–9(–14) cm long, 0.5–4(–8) cm wide, open, upper panicle branches ascending or reflexed, usually on a well exerted peduncle; inflorescence branches solitary at each node, with (6–)8–12(–13) nodes per inflorescence; branches usually lax, occasionally ascending, seldom appearing contracted. Pedicels (0.5–)0.7–1.3(–1.9) mm long, minutely setose. Spikelets (2.4–)2.6–3.2(–3.5) mm long, usually not appearing densely placed on branches, 3–30 spikelets per branch. Glumes (1.0–)1.2–1.6(–1.9) mm long, equal or second glume slightly longer than first, acute,  $1/3$ – $1/2$  the length of the floret, usually dark green, one-nerved. Lemmas (2.2–)2.4–3.0(–3.3) mm long, rounded and tapering to an acute apex, glabrous or occasionally scabrous, dark green, 3-nerves obscure. Paleas (2.2–)2.4–2.8(–3.1) mm long, about equal to the lemma, glabrous, dark green. Anthers (1.4–)1.6–2.0(–2.1) mm long, dark green at maturity. Caryopses 1.4–1.6 mm long, 0.7–0.9 mm wide, elliptical to slightly ovate, greenish-brown. Chromosome number  $2n = 40$  (Reeder 1967).

*Distribution*.—Valley of Mexico, and Guatemala. Moist soils in meadows, hillsides, or ditches. This species has often been misidentified as *M. richardsonis*. However, it differs by its larger spikelets, open inflorescence, and flat or folded leaf blades.

3. **Muhlenbergia repens** (J. Presl) Hitchc., In: Jepson, Fl. Calif. 1(3):111. 1912. BASIONYM: *Sporobolus repens* J. Presl, Rel. Haenk. 1:241. 1830. *Vilfa repens* (J. Presl) Trin., Mem. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 4(1):102. 1849. TYPE: MEXICO, *Haenke s.n.* (HOLOTYPE: PR!; Type fragment: US!; ISOTYPE: MO!).



*Muhlenbergia subtilis* Nees, *Linnaea* 19:689. 1847. TYPE: MEXICO, *Aschenbom* 206 (HOLOTYPE: B-lost; Type fragment: US!). *Muhlenbergia abata* I.M. Johnston, J. Arnold *Arbor.* 24:387. 1943. TYPE: NEW MEXICO. Valley of the Rio Grande, *Wright* 1982 (HOLOTYPE: GH!). Hitchcock's name of *M. repens* was incorrectly circumscribed when he transferred the name from *Sporobolus*. However, he did not explicitly exclude the type and in later publications corrected his error. Johnston provided a new name for this species assuming that Hitchcock's name was a later homonym of *Sporobolus repens* J. Presl and thus illegitimate.

Perennial with creeping, scaly rhizomes; rhizome scales (3–)5–9(–20) mm long, acute, often deteriorating with age. Culms (5–)8–20(–42) cm long, 0.3–0.6(–1.1) mm diam., decumbent and usually forming dense mats, freely branching above, glabrous; internodes 4–16(–50) mm long, variable, lightly nodulose roughened below inflorescence, usually smooth on lower culm internodes. Sheaths (2–)6–14(–34) mm long (occasionally longer), shorter to longer than internodes, margins hyaline, overlapping at base, open near collar and diverging from culm near collar. Ligules (0.1–)0.4–1.0(–1.8) mm long, membranous, truncate, decurrent, occasionally becoming split. Blades (0.4–)1.1–3.0(–6.0) cm long, (0.5–)0.7–1.5(–4) mm wide, glabrous, involute, straight or usually arcuate to spreading, midvein absent, margins scabrous. Inflorescence a panicle, 1–4(–9) cm long, 1–6(–32) mm wide, contracted, usually included at base in uppermost leaf sheath; inflorescence branches solitary at each node with (3–)4–8(–10) nodes per inflorescence; branches usually ascending, rarely lax. Pedicels (0.2–)0.5–1.5 mm long (rarely longer), minutely setose. Spikelets 2.7–3.3(–3.6) mm long (sometimes longer), usually with one floret, occasionally two, not densely distributed, 1–7(–19) spikelets usually on lowermost panicle branch. Glumes (1.1–)1.6–2.4(–3.6) mm long, about equal or first a little longer, acute, 1/2 to equaling length of floret, usually light green, 1-, 2-, or 3-nerved. Lemmas 2.6–3.2(–4.2) mm long, acute to attenuate, often narrowing into a mucro or short awn, 3-nerved, appearing glabrous or scabrous along midnerve apically, occasionally short hairs are visible near base or along margins, opaque to dark green or mottled; awn 0.1–0.3(–1.4) mm long. Paleas 2.1–2.7(–3.4) mm long, appearing glabrous or scabrous between the two nerves, color similar to lemma. Anthers (0.7–)1.0–1.4 mm long, yellow, becoming purple at maturity. Caryopses 1.1–1.5 mm long, 0.4–0.7 mm wide, elliptic to ovate, brown, usually with a straw colored coating on pericarp. Chromosome number  $2n = 60$ , 70–72 (Brown 1951; Morden 1985; Reeder 1967, 1968).

*Distribution.*—Southwestern United States and northern Mexico south through the Valley of Mexico to Chiapas. On open sandy grounds of dry meadows, canyon bottoms, and along roadsides, often forming dense stands. Soils are variable, ranging from alkaline to calcareous and heavily gypsiferous.



This species is similar to *M. utilis* in many respects, such as vegetative characteristics and the nature of the caryopsis. However, *M. utilis* can be distinguished by its smaller spikelets, more slender culms and spreading blades. Some populations tend to show intergradation with *M. richardsonis*. Vegetative apomixis in this species has been previously reported (Morden & Hatch 1986).

4. ***Muhlenbergia richardsonis*** (Trin.) Rydb., Bull. Torrey Bot. Club 32:600. 1905. BASIONYM: *Vilfa richardsonis* Trin., Mem. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 4(1):103. 1840. *Sporobolus richardsonis* (Trin.) Merr., Rhodora 4:46. 1902. *Muhlenbergia brevifolia* (Scribn.) Jones var. *richardsonis* (Trin.) M.E. Jones, Contr. W. Bot. 14:12. 1912. TYPE: NORTH AMERICA, *Richardson s.n.* (HOLOTYPE: LE!; Type fragment: US!).

*Muhlenbergia aspericaulis* Nees ex Trin., Mem. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 4(1):103. 1840 pro syn. *Sporobolus aspericaulis* (Nees ex Trin.) Scribn., Bot. Gaz. 21:15. 1896. TYPE: *Richardson s.n.* (HOLOTYPE: BM; Type fragment: US!). The types of the basionyms *Vilfa richardsonis* Trin. and *Muhlenbergia aspericaulis* Nees ex Trin. may be the same. *Vilfa squarrosa* Trin., Mem. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 4(1):100. 1840. *Muhlenbergia squarrosa* (Trin.) Rydb., Bull. Torrey Bot. Club 36:531. 1909. TYPE: Menzies Island, Columbia River, Washington, Northwest America *Douglas s.n.* (HOLOTYPE: LE!; Type fragment: US!).

*Vilfa depauperata* Torr. in Hook., Fl. Bor. Amer. 2:257, pl. 236. 1840. *Sporobolus depauperatus* (Torr.) Scribn., Bull. Torrey Bot. Club 9:103. 1882. TYPE: sandy parts of Columbia River, from Menzies Island upward, *Douglas s.n.* (HOLOTYPE: K; Type fragment: US!; ISOTYPE: GH!, NY!). Not *Muhlenbergia depauperata* Scribn. (Bot. Gaz. 9:187. 1884).

Perennial with scaly rhizomes, often a knotty base, mat-forming; rhizome scales (4–)6–9(–13) mm long, acute, often deteriorating with age. Culms typically (5–)10–30(–64) cm tall, occasionally taller, 0.3–0.6(–1.1) mm diam., wiry, glabrous, decumbent or erect, freely branching above or not; internodes (4–)11–40(–94) mm long, variable, variously nodulose-roughened, occasionally appearing smooth. Sheaths usually (1–)9–22(–50) mm long, shorter or longer than internode, margins hyaline, overlapping at base, open near collar and diverging from culm. Ligules (0.5–)1.0–1.9(–3.0) mm long, membranous, acute to truncate, erose, or shallowly toothed. Blades (0.4–)1.6–4.0(–6.5) cm long, (0.5–)1.0–1.6(–4.2) mm wide, flat or becoming involute when desiccated, straight or usually arcuate-spreading, midvein absent, margins scabrous. Inflorescence a panicle, (1–)2–5 cm long (rarely up to 15 cm), 1–4(–17) mm wide, contracted, usually on a well-exserted peduncle, inflorescence branches solitary at each node, (4–)7–12(–18) nodes per inflorescence; branches usually ascending, seldom lax. Pedicels (0.2–)0.5–1.1(–2.0) mm long, minutely setose. Spikelets (1.7–)2.1–2.7(–3.2) mm long, with one floret, rarely two, crowded on branches, 1–13(–40)



spikelets on lowermost panicle branch. Glumes (0.6–)0.9–1.4(–2.0) mm long, about equal or second slightly longer, acute,  $1/3$ – $1/2$  the length of floret, green, 1- (rarely 2-) nerved. Lemmas (1.7–)2.0–2.6(–3.1) mm long, acute or acuminate, often mucronate, glabrous or scabrous near apex, usually dark green or mottled, 3-nerves obscure, mucro 0.1–0.2 mm long. Paleas (1.0–)1.8–2.4(–2.9) mm long, glabrous or scabrous between nerves, color similar to lemma. Anthers (0.9–)1.2–1.4(–1.6) mm long, yellow, becoming purple at maturity. Caryopses (0.9–)1.1–1.4(–1.6) mm long, 0.3–0.5(–0.6) mm wide, narrowly elliptic, brown. Chromosome number  $2n = 40$  (Delay 1950; Morden 1985; Stebbins & Love 1941).

*Distribution*.—This is the most widely distributed species of the complex occurring from New Brunswick and Maine, west to Alaska, south through the Sierra Nevada Mountains into Baja California, and the Rocky Mountains to New Mexico and Arizona. On open soils of moist meadows or drier sites away from saturated soils, sandy arroyo bottoms, occasionally alkaline soils.

*Muhlenbergia richardsonis* is similar to *M. repens* with which there appears to be some intergradation in the southwestern United States. There are two intergrading forms of *M. richardsonis*. One form, which has been referred to as *M. squarrosa*, has stout, decumbent, and spreading culms and occupies drier sites with little competition from other species. The other form, referred to as *M. richardsonis*, has more slender, erect culms and is usually growing in moister soils in a meadow-like association. This species is often confused with *M. cuspidata* (Torr.) Rydb. from the Midwestern U.S., which differs by lacking rhizomes and which has puberulent culm internodes, a shorter ligule, and long glumes which are acuminate or cuspidate. *Muhlenbergia filiformis* (Thurb.) Rydb. is an annual or weak perennial resembling *M. richardsonis*, but is distinguishable by its non-nodulose roughened culms and ovate to acute glumes (these often slightly erose or ciliate along the margins).

##### 5. *Muhlenbergia utilis* (Torr.) Hitchc., J. Wash. Acad. Sci. 23:453. 1933.

BASIONYM: *Vilfa utilis* Torr., U.S. Rep. Expl. Miss. Pacif. 5:365. 1858. *Sporobolus utilis* (Torr.) Scribn., U.S.D.A. Div. Agrostol. Bull. 17:17 1. f. 467. 1899. TYPE: Lost Mt. Spring, trip from Tejon to the Lost Hills, Calif., in stony places, Blake *s.n.* (HOLOTYPE: NY!; Type fragment: US!; ISOTYPES: GH!, MO!).

*Vilfa sacatilla* E. Fourn., Mex. Pl. 2:101. 1886. *Sporobolus sacatilla* Griseb. ex E. Fourn., Mex. Pl. 2:101. 1886 pro syn. TYPES: Chapultepec pr. Mexico, Schaffner 165 pl. ed Hohen. (W); San Luis Potosi, Virlet 1455 (P); Texas, Wright (in herb. Durand, P). (TYPE fragments: US!). Fournier (1886) also listed *Agrostis brevifolius* Nutt. as a synonym. However, this is a synonym of *Muhlenbergia cuspidata* (Torr.) Rydb.

Perennial with scaly rhizomes; rhizome scales (3–)5–9(–13) mm long,



acute; scales often deteriorating with age. Culms 7–20 cm high, 0.2–0.6(–0.9) mm diam., much branched above, erect on smaller plants, decumbent, long and trailing on larger plants, up to one meter long, usually ascending, glabrous; internodes (3–)8–22(–37) mm long, variable, lightly nodulose roughened or with siliceous markings below inflorescence, smooth or not as pronounced on lower internodes. Sheaths (3–)7–13(–24) mm long, shorter or longer than internodes, margins hyaline, overlapping at base, open near collar and diverging from culm. Ligules (0.2–)0.3–0.5(–0.8) mm long, membranous, truncate, decurrent. Blades (5–)11–24(–47) mm long, (0.2–)0.8–1.3(–1.8) mm wide, glabrous, flat or mostly involute, straight or becoming arcuate with age, blades of major culms often at right angles to culm, midvein absent, margins scabrous. Inflorescence a panicle, 1–3 cm long (rarely longer), 1–4 mm wide, contracted, usually included at base in uppermost leaf sheath; inflorescence branches solitary at each node, with 3–13 nodes per inflorescence; branches ascending, occasionally becoming lax. Pedicels (0.1–)0.2–0.6(–1.1) mm long, glabrous. Spikelets (1.4–)1.6–2.0(–2.3) mm long, with one floret, these crowded on branches, (1–)2–7(–14) spikelets on lowermost panicle branch. Glumes (0.5–)0.6–1.0(–1.4) mm long, about equal, acute,  $1/3$ – $1/2$  length of floret, straw colored to light green, 1- or 3-nerved. Lemmas (1.3–)1.5–2.0(–2.3) mm long, 3-nerved, acute, not mucronate, green or purple near base at maturity, glabrous, rarely with short hairs present. Paleas (1.0–)1.4–1.8(–2.0) mm long, glabrous, color similar to lemma or with more purple at maturity. Anthers (0.7–)1.0–1.2(–1.4) mm long, yellow, becoming purple at maturity. Caryopses (0.7–)0.8–1.0(–1.2) mm long, 0.4–0.6 mm wide, elliptic to ovate, brown, usually with straw-colored coating on pericarp. Chromosome number  $2n = 20$  (Gould 1966; Morden 1985).

*Distribution.*—United States: Arizona, southern California, Nevada, and central Texas; Mexico: Chihuahua, Coahuila, Durango, Guanajuato, Jalisco, Mexico, Nuevo Leon, Puebla, Sonora, and Veracruz; Guatamala. In wet soils, usually with slow flowing fresh water or along margins of faster flowing streams or rivers, depressions in grasslands, and alkaline or gypsiferous plains.

This species is similar to *M. repens* from which it differs by its more wiry culms, slender leaves, shorter ligules, and smaller spikelets. This species was used by people of Mexico for stuffing packsaddles, hence the common name “aparejo grass.”

6a. *Muhlenbergia villiflora* Hitchc. var. *villiflora*, see Morden 1996 (p. 29).

6b. *Muhlenbergia villiflora* Hitchc. var. *villosa* (Swallen) Morden, see Morden 1996 (pp. 29, 30).



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